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Ecology, 89(2), 2008, pp. 585–587

BIOMASS AND TOXICITY RESPONSES OF POISON IVY (TOXICODENDRON RADICANS) *TO ELEVATED ATMOSPHERIC CO_2: REPLY*

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Manuscript received 24 April 2007; accepted 20 June 2007; final version received 18 September 2007. Corresponding Editor: B. A. Hungate.

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Schnitzer et al. (2008) contrast results from a recent experimental study documenting increased growth of poison ivy (*Toxicodendron radicans*) in the free-air carbon dioxide enrichment (FACE) facility in the Duke Forest, North Carolina (Mohan et al. 2006), to an uncontrolled observational study finding decreased abundance of poison ivy in Wisconsin forests between 1959 and 2005 (Londré and Schnitzer 2006). Schnitzer et al. (2008) accurately point out that controlled field studies may not always emulate long-term responses in uncontrolled "real world" forests. The lack-of-change in overall vine abundance in the Wisconsin forests is in contrast to previous studies showing recent increases in the abundance of vines in temperate (Myster and Pickett 1992, Dillenburg et al. 1995, Allen 2007, Allen et al. 2007) and tropical forests (Laurance et al. 2001, Phillips et al. 2002, 2005, Wright et al. 2004), as well as our Duke FACE poison ivy study that suggests increases in vine growth at elevated atmospheric CO_2. Data from the Duke experiment highlight the impact of deer and rabbit herbivory for understory plants, and a recent deer-exclosure study (Forrester et al. 2006) cited by Schnitzer et al. (2008) suggests that the difference between our studies may stem from mammalian herbivory on poison ivy. We additionally address the idea that understory light limitation may explain the differential responses of poison ivy in the two studies.

Londré and Schnitzer (2006) compare abundances of woody vines (lianas), including poison ivy, in 14 southern Wisconsin forests in 2005 with abundances previously recorded in 1959. The authors found that the overall abundance of vines was not different between the two years, and that poison ivy was actually less abundant in 2005 than it was in 1959. Schnitzer et al. (2008) point out that any observed differences between these two years could be due to many potential causes, such as successional development, degree of fragmentation, increasing temperatures, rising atmospheric CO_2, or increasing deer populations, as well as land use histories, nitrogen deposition, increasing atmospheric ozone, and other changes over time including a host of unknown variables.

Schnitzer et al. (2008) present several mechanisms to potentially reconcile differences in the results from the Duke FACE experiment with their observations in the Wisconsin forests, including deer herbivory and light limitation. We believe mammalian herbivory is largely responsible for the different responses of poison ivy in the two studies, as the Duke poison ivy plants were protected from deer and rabbits while the Wisconsin plants were not. The negative impacts of overly abundant mammalian herbivores on forest understory plants are well known (Leopold et al. 1947, Alverson et al. 1988, DeSteven 1991, Alverson and Waller 1997, Augustine and Jordan 1998, Opperman and Merenlender 2000, Terborgh et al. 2001). As Schnitzer et al.

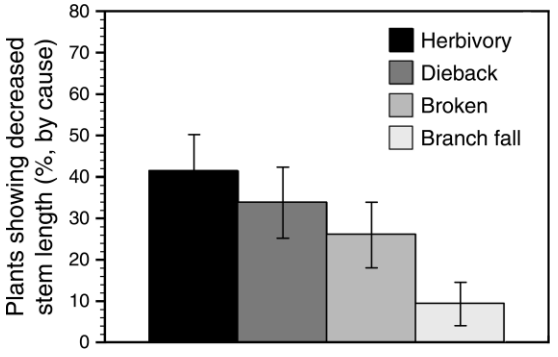

FIG. 1. Causes of decreased stem lengths (heights) between autumn 1996 and spring 1997 (the initiation of the Duke FACE experiment) in the FACE forest understory. Bars represent percentages (mean ± SE) of "shrunken plants" (understory trees, shrubs, and vines) that exhibited symptoms of mammalian herbivory, stem dieback, broken stems, or stems snapped by fallen canopy tree branches. When only poison ivy stems were analyzed, the percentage of stems preyed upon by mammals increased to 88%. Mammalian herbivory data presented here may be biased toward rabbit herbivory; rabbits possess both upper and lower incisors and cut stems at a 45° angle, leaving very distinctive bite signatures. Deer lack upper incisors and tear or rip plant stems; deer herbivory can be difficult to distinguish from other causes of stem breakage, so the "broken" data likely include stems that were eaten by deer. "Dieback" represents stems with the terminal portion still present but dead and is often a sign of fungal (or other) pathogens or drought stress.

(2008) report, a two- to fivefold increase in Wisconsin deer populations has occurred over the last 40 years, and the deer population in North Carolina tripled between 1983 and 1998 (data *available online*),[10] particularly in forests like the Duke FACE, which are adjacent to urban and suburban development (information *available online*).[11] Poison ivy is a favorite forage crop of many wildlife species including white-tailed deer and rabbits (Gillis 1971, Hoppes 1988, Penner et al. 1999, Suthers et al. 2000). Forrester et al. (2006) found that poison ivy abundance increased fourfold after 16 years of deer exclusion (due to the small sample size, none of the plant species in this study exhibited statistically significant responses to deer exclusion), and poison ivy was one of only three species whose abundance declined significantly in response to increasing deer populations before the exclosure study began. Similarly, recent work in two temperate South Carolina forests, where habitat change and human hunting has maintained stable or even declining deer populations since the mid-1990s (data *available online*),[12] documents increased density and growth of poison ivy during the last 12–22 years (Allen 2007, Allen et al. 2007).

At the Duke FACE experiment we are finding that mammalian herbivores mediate some plant responses to atmospheric CO_2 (Figs. 1 and 2). Poison ivy plants accessible to deer and rabbits show no statistically significant effect of CO_2 on survivorship. However, these unprotected plants exhibit much higher mortality rates than their herbivore-protected (caged) counterparts (Fig. 2). The high mortality rates of poison ivy plants available to herbivores, and the potential for such plants growing at elevated CO_2 to have higher mortality than ambient-grown plants, may help explain the declining poison ivy cover in Wisconsin forests.

Schnitzer et al. (2008) also reason that the understory of the older Wisconsin forests may offer a lower light environment than the Duke Forest, and that greater light limitation may have increased the mortality of poison ivy plants and reduced their abundance in the northern forests. Schnitzer et al. present no data for light intensities in the Wisconsin forests, but understory light levels at the loblolly pine plantation at FACE, often <2–3% full sunlight (Mohan et al. 2007), are unlikely to be substantially different from the Wisconsin stands.

The works of Londré and Schnitzer (2006) and Schnitzer et al. (2008) highlight the limitations of both controlled experiments and purely observational studies,

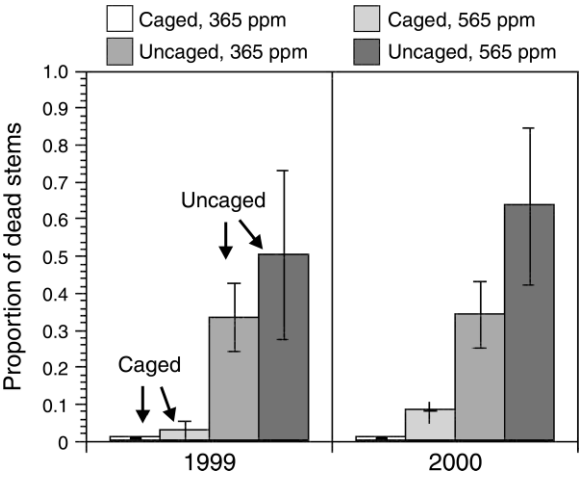

FIG. 2. Cumulative mortality (mean ± SE) of poison ivy stems (ramets) growing in the Duke Forest FACE experiment ($n = 3$ plots/treatment). "Caged" plants (paler gray) are plants protected from mammalian herbivores; "uncaged" plants are available to both deer and rabbit herbivores. Note the high mortality of uncaged plants at both CO_2 concentrations. Whether or not a plant was accessible by herbivores highly influenced its mortality probability ($P < 0.0001$). Although there is no significant CO_2 effect on mortality, there is an important $CO_2 \times$ cage interaction ($P = 0.026$), suggesting that the effects of herbivores on poison ivy mortality is influenced by atmospheric CO_2 concentrations. Caged plants growing at ambient CO_2 had 0% mortality in years 1999 and 2000.

[10] ⟨http://www.env.duke.edu/forest/forest/wildlife.htm⟩

[11] ⟨http://www.ncwildlife.org/pg07_wildlifespeciescon/pg7b4.htm⟩

[12] ⟨http://www.dnr.sc.gov/news/Yr2007/june25/june18_harvest.html⟩

and the value of long-term ecological data. Clearly, uncontrolled observational studies can reveal important changes in ecosystem structure over time and may suggest potential reasons for differential behavior of natural ecosystems, but controlled experiments are required to determine the underlying, mechanistic reasons for change. By combining the observational work in Wisconsin and the controlled CO_2 and herbivory experiments at Duke, we gain insights regarding the importance of top-down control for structuring ecological systems in an increasing-CO_2 world.

Acknowledgments

We thank J. M. Melillo, P. T. Frankson, and K. J. Lenoir for helpful comments on this manuscript. We thank D. LeBauer for critical field assistance at Duke FACE. This work was enhanced by discussions with M. Dietze, J. Hille Ris Lambers, I. Ibañez, S. LaDeau, J. McLachlan, R. Peet, J. Pippen, B. Strain, and M. Wolosin. The manuscript was improved by suggestions from an anonymous reviewer. This work was supported by the Office of Science (BER), U.S. Department of Energy, Grant Number DE-FG02-95ER62083 and Terrestrial Ecosystems and Global Change (TECO) Grant Number DE-F602-97ER62463.

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